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Voltage Gradients of Trees as an Indicator of Susceptibility to Insect Attack

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Introduction:- Forest entomologists have, for a number of years, been attempting to find a method of estimating the susceptibility of trees to insect attack. This is particularly true in regards to certain bark beetles and borers. To this end Person (1928, 1931) worked on the chemical changes which occur in a tree to make it attractive to bark beetles, and Keen (1936) was able to formulate a method of ocular estimation of tree susceptibility for ponderosa pine (Pinus ponderosa Doug.) in relation to the western pine beetle (Dendroctonus brevicomis Lec.) Hall (1933) showed that factors other than the bronze birch borer were of primary importance in the decadence of hardwood stands after logging, and that such decadence could be estimated by ocular methods. To date, no method of estimating physiological changes or decadence before they became evident in the external appearance of the trees, has been advanced.

The writer has held the opinion for a number of years that the voltage gradient of a tree, or a portion of a tree, might possibly be used as an index of susceptibility. That is, that the physiological condition of a tree which would make it attractive to insects such as certain bark beetles or borers, might be reflected in the voltage gradients. Recently, suitable equipment has become available, and during the past season portable equipment has been used in the field. It is believed that the results of these studies are of sufficient significance to justify publication. It is hoped that other workers may, by the results presented, be induced to add this tool to their research equipment.

Historical.--The concept that there are direct current voltage gradients in living organisms is not new. In fact their presence in both plants and animals has been amply demonstrated for some time, both here and abroad. Exactly how those findings are to be interpreted is still a matter for discussion. The claim to originality here presented is the application of these potential gradients to the present problem. It is not the purpose of this paper to make an exhaustive survey of the literature on the subject, but the work of Lund and his co-workers may be pointed to as being most pertinent to present discussion.

Briefly, Lund (1928 and subsequent papers) showed that the voltage gradient in the Douglas fir, in the external circuit was, normally, electropositive toward the tip of the tree, negative toward the base; that it fluctuated and even reversed; that it was roughly proportional to the distance apart that the electrodes were placed on the stem or branch; that it was affected by such factors as light, temperature, etc.; and that it was of such magnitude as to be readily detectible on instruments of moderate sensitivity. Most of these findings can now be substantiated from both field and laboratory experiments on growing trees.

Experimental Procedure.-- With the advent of the Burr, Lane, Nims vacuum tube voltmeter, it seemed possible that we had an instrument which was adaptable to the type of experiments which we wanted to perform. Accordingly, an arrangement of a Leeds and Northup Amplifier, with a Type K-1 potentiometer and a box type galvanometer was set up, using silver-silver chloride electrodes. The arrangement worked very well in the laboratory, but proved too heavy and difficult to transport for any extensive field work. Dr. Nims then became interested in the problem and constructed a relatively small, self-contained vacuum tube voltmeter (Fig. 1) which is fully described in an accompanying paper Goodwin (Nims, Parr, 19-). This instrument has proved very satisfactory during the past season. It is easily portable, has an adequate voltage range, and may be constructed at moderate expense by anyone moderately familiar with such equipment.

Silver-silver chloride electrodes of the type described by Renshaw (1940) have been used with satisfactory results when calibrated against a standard pair, for changes in temperature.

In the present work all readings have been taken with the electrodes placedon, or approximately on, the cabium. This is accomplished by removing two small pieces of bark and phloem, and applying the electrodes to the ambium through these holes (Fig. 2). The electrodes are placed in small blocks and the blocks held to the tree by rubber bands. Readings have been taken on trees from one-half inch up to 26 inches in diameter. Only a few minutes are required for a reading on any onetree.

Results, Laboratory Experiments.-- During the summer of 1939, experiments were carried out on potted pine trees. Pitch pine (Pinus rigida Mill.) was used in these experiments since that species is hardy and will stand rather severe manipulation without being killed. These tests showed conclusively that the voltage gradient followed the growth activities of the trees closely. Using the large apparatus described above, with the instrument box shielded and grounded, and the pot containg the tree insulated, voltage gradients of from minus 5.0 millivolts to a plus 20.0 millivolts were obtained with the electrodes placed one inch apart on the main stem, depending on the condition of the tree. As referred to in this paper, a positive reading means that the upper electrode, or the one placed closest to the growing tip is electro-positive to the basal, when the electrodes are placed one above the other longitudinally at approximately the position of the cambium on the main stem. A negative reading indicates that the upper electrodes is negative to the basal. This is on living material. After a tree is dead the voltage gradient may become either positive or negative, and may vary sharply within a short time. Such readings may be obtained from a post or stick.

Typically, when growth started on these trees, the voltage gradient averaged about plus 12.0 millivolts, but in some cases went as high as 15.0 or 20.0 millivolts. During the summer the gradient dropped to an average of approximately 7.0 millivolts, and as the growing tissues became mature, gradually became lower until it remained at a plus 2.0 to 3.0 millivolts. On other trees placed out of doors for hardening, the gradient reversed in the fall and became minus 3.0 to 5.0 millivolts, and when growth was again resumed in the spring of 1940, this gradient rose to a plus 7.0 to 8.0 millivolts. No diurnal reversal of gradient was noted on those trees in the laboratory as described by Lund (1930, 1931). When a tree was allowed to die, the gradient dropped to zero, then became negative, and after that varied from negative to positive at irregular intervals as described for a stick. What field experiments were made at that time partially substantiated these findings.

It was found that both withholding water, and drowning the tree produced much the same results except that the recovery from the effects of smothering in water, as indicated by the voltage gradient, required much longer than was necessary for recovery after withholding water.

Results, Field Experiments.--As soon as the portable equipment was constructed in the spring of 1940, readings were begun on trees of various sizes in the field. The greater portion of these readings were made on red and white pines (Pinus resinosa Ait. and Pinus strobus L.) at the Rainbow Plantations of the Connecticut Agricultural Experiment Station, Windsor and East Granby, Conn., and on red pine at the Saltonstall plantations of the New Haven Water Company at Branford, Conn. Some readings were made on beech (Fagus grandifolia Ehrh.) at Hunterbrook Park in Westchester County, New York, and others on spruce (Picea rubra Link) in Vermont and New Hampshire and on white pine in Maine. With the exception of September and October, when only a few observations were made at Rainbow and Saltonstall plantations, readings were taken on a rather large series of trees from the third of June throughout the summer. Two types of electrodes have been used with equal success in these experiments. The first, as described by Burr, Lane, and Nims (1936) with the electrodes themselves set in agar made up in normal sodium chloride solution; and the second, of the type used by Renshaw, as mentioned previously. All readings were made longitudinally in the cambial region of the trees, with the distance between the electrode points standardized at one inch. The sensitivity of the instrument was set at one millivolt per millimeter of deviation on the galvanometer scale.

Space does not permit the inclusion of the data obtained from all of the trees during the summer. Graphs of typical trees, both normal and sub-normal, are shown in the following figures.

Tree number 1 was a white pine, slightly over 4 inches in diameter at breast height and between 25 and 30 feet tall. It was infested with Pityophthorus sp. and Ips pini. On June 3 the new growth had started, however, and the crown appeared to be in good condition. Although the gradient was oriented in the normal direction (upper electrode positive) on June 3, the reading (1.5 millivolts) was considerably lower than the other white pines at that time. On June 14 the reading was zero and after that became negative, as is the case with dead material such as a post, where it remained, with the exception of one reading, until early in August (figure 3). Readings were discontinued on that tree at that time because it was obviously dead. The cambium was turning brown and the crown was beginning to fade slightly.

Tree number 2 was also a white pine, an inch larger in diameter than number 1, and somewhat taller. That tree was uninfested and perfectly normal in appearance. The reading on June 3 was plus 3.5 millivolts, and although the voltage gradient varied throughout the summer, it remained on the positive side of the scale until after August 14, when it became negative, as did the other normal trees in the stand (figure 4).

Tree number 5 was a red pine, slightly over 7 inches in diameter and about 30 feet in height. It became infested in 1939 with Ips calligraphus and Dendroctonus valens, but on June 3 the crown appeared to be in good condition. The reading on June 3 was 4.5 millivolts, with the upper electrode positive, i. e., the gradient was normally oriented but somewhat lower than uninfested trees of that species. The voltage gradient fell rapidly, became negative on June 19, and remained in that orientation until August 8, when reversals in the opposite direction were taking place in the normal trees in the stand. It remained positive after that time (figure 5). Although the crown of the tree still appeared in good condition on October 24, it is highly probable that the tree will die (the crown will fade) during 1941.

Tree number 6 was a red pine the same size as number 5, but uninfested. The reading on June 3 was 8.0 millivolts, with the top positive to the base. The tree was shedding pollen at the time and it has been found that when such a condition exists, the voltage gradient is somewhat higher than is the case with trees not shedding pollen. The voltage gradient fell throughout the summer, as was the case with other healthy trees, remaining oriented with the top positive to the base until August 8, at which time it became reversed, and remained so through October 24 (Figure 6).

Tree number 16 was a white pine, badly suppressed, one and one-quarter inches D.B.H., and 11 feet in height. It was uninfested. On June 28, when the first reading was made on it, the voltage gradient was 5.5 millivolts, with the top positive to the base. The reason for the high reading on that tree at the time is probably due to the fact that new growth started at a later date than on the

other trees and new shoots were just being put out at that time. On July 24 the voltage gradient on that tree was reversed, the base was positive to the top, and the reading was minus 4.0 millivolts. This was rather disturbing, as the tree appeared to be perfectly healthy. The voltage gradient remained reversed until August 14, when the rest of the stand was reversing, when the top again became positive to the base (Figure 7). On October 24, the foliage on that tree had turned yellow, the cambium was brown nearly to the ground and the tree was obviously dead, probably from suppression. This bore out other evidence that had been accumulating that a tree might be physiologically dead before it was apparent to the eye, and that it might be possible to determine such a fact with this instrument.

On August 27, a stand of spruce in the Crawford Notch area of the White Mountains of New Hampshire was found where a number of trees had died from infestations by the spruce bark beetle, Dendroctonus piceaperda Hopk. A few trees were found in which attacks were just taking place and the insects were boring into the bark but had not reached the cambium. The readings from several such trees, representative of the group, and from several of the representative normal trees in the stand, are presented in the following table:

Table I. Voltage Gradients on Normal Trees and Trees Recently Attacked by D. piceaperda, Crawford Notch, New Hampshire

Date	Species	Condition	Voltage gradient	
8/27/40	Spruce	New attack	- 3.0 MV	Top negative to base
8/27/40	"	" "	- 2.5 MV	Top negative to base
8/27/40	"	" "	- 3.6 MV	Top negative to base
8/27/40	"	" "	- 3.0 MV	Top negative to base
8/27/40	"	Normal	+ 2.5 MV	Top positive to base
8/27/40	"	"	+ 1.8 MV	Top positive to base
8/27/40	"	"	+ 2.4 MV	Top positive to base
8/27/40	"	"	+ 2.0 MV	Top positive to base

It will be noted that the top was still positive to the base on normal trees on August 27. In other words, the reversalof voltage gradient occurred at an earlier date in southern New England than was the case some 300 miles farther north. It is interesting to note that there was no evidence of insect attack on any trees in this group, as evidenced by boring dust, holes in the outer bark, or pitch tubes, unless those trees deviated from the normal as indicated in the above table.

Late in September readings were taken on a number of spruces that had been defoliated in varying degrees by the European spruce sawfly (Gilpinia polytoma Htg.). This was the first of a series of such readings planned on hosts attacked by a primary insect. Even in a single set of readings it was possible to detect wide differences in the condition of the trees as an effect of partial defoliation by that insect. This is perhaps best shown in the following table, which constitutes a representative sample of trees in two different groups:

Table II. Voltage Gradients on Partially Defoliated and Undefoliated Spruces, Wilmington, Vermont

Defoliated		Undefoliated (Sprayed)	
Tree No.	Voltage gradient	Tree No.	Voltage gradient
621	+ 6.0 MV	663	- 1.0 MV
632	+ 7.2 "	664	- 1.6 "
630	+ 5.6 "	662	- 1.2 "
619	+ 5.0 "	660	- 0.6 "
647	+ 5.8 "	659	- 2.0 "
		661	- 1.2 "

It will be noticed at once that whereas the trees in the sprayed plot were normal in that the voltage gradient had reversed and the top become negative to the base, as was to be expected, the trees which were partially defoliated presented the picture of being in a rather early summer condition so far as the voltage gradient was concerned. Just what will happen in this and nearby stands where other readings were made is to be determined in the spring and summer of 1941.

Discussion.--It is apparent from the material presented that it is possible to obtain rather consistent voltage gradients from living trees. From work done during the past season, it has gradually become evident that these gradients vary comparatively little between trees of different size and age or between trees of different species, although there does seem to be a small but rather constant difference between red and white pine. Numerous tests have shown that there is little difference between red and white pine. Numerous tests have shown that there is little difference between a reading taken on one side

of a tree as opposed to a reading taken on the opposite side, as long as the electrode points are placed an equal distance apart and are located one above the other in both instances. The voltage gradient appears to follow a definite cycle in all species tested, being rather high in the spring when growth starts, falling throughout the summer with a slight rise when secondary growth starts, then gradually falling to reverse polarity with the base positive to the top late in the summer. In the case of subnormal trees it seems evident that the cycle is at least partially reversed from that found in normal trees. That is, if the top was positive to the base in the spring, the gradient rapidly reversed, the base remained positive to the top during most of the summer and then reversed again.

The importance which this may have to entomological problems is evident. If it is possible to tell, and apparently such is the case, when a tree has reached a physiological condition where that tree is susceptible to secondary insect attack, thenit would be possible to eliminate such trees from a stand. Insuch an instance trees number 1, 5, and 16 would have been removed, as would the spruces in the Crawford Notch area with a negative reading indicated in table I.

Where primary insects such as defoliators are concerned, indications are that it will be possible to determine when trees have passed the point where they will recover, and when they will reach a condition where they may be attacked by secondary insects. It is probably not assuming too much to say the same for stands affected by other factors such as drought.

The reason for the reversal of polarity at the end of the summer is not yet clear. It can be said,however, that it coincides with the storage of food in the form of fat in the plant tissues. From simple colorimetric and sponification tests on some of this material, it is apparent that as the gradient reverses, the percent of fat stored becomes higher and continues to increase as the base becomes more and more positive in respect to the top of the tree. This is one of the problems to be worked upon inthe immediate future.

Little has been said of deciduous trees. What observations have been made on some four or five species indicate that the voltage gradients inthem follow the same trends and are of about the same magnitude as those in conifers.

The writer wishes to express his gratitude to Professor H. S. Burr of the Schoolof Medicine, Yale University, for several suggestions and to Dr. L. F. Nims of the same institution for constructing the vacuum tube voltmeter used in this work and for timely suggestions in its use.

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Figure 1. Portable vacuum tube millivoltmeter as set up for readings on trees in the field.

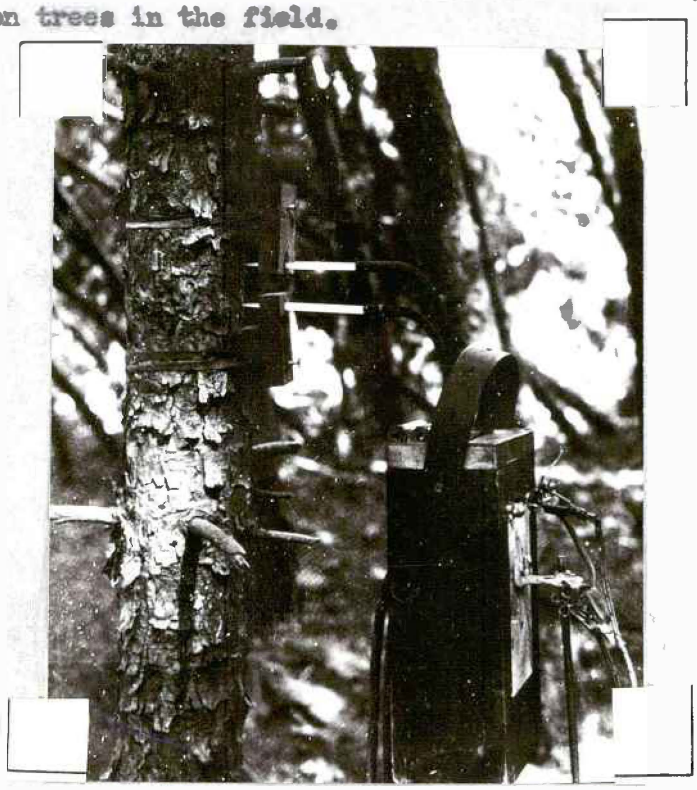

Figure 2. Silver-silver chloride electrodes in place on the cambium of a tree for field readings. In these electrodes the chloridized wire is not set in agar in the small glass tube applied to the cambium, but in the box connected by agar-filled rubber tubes.

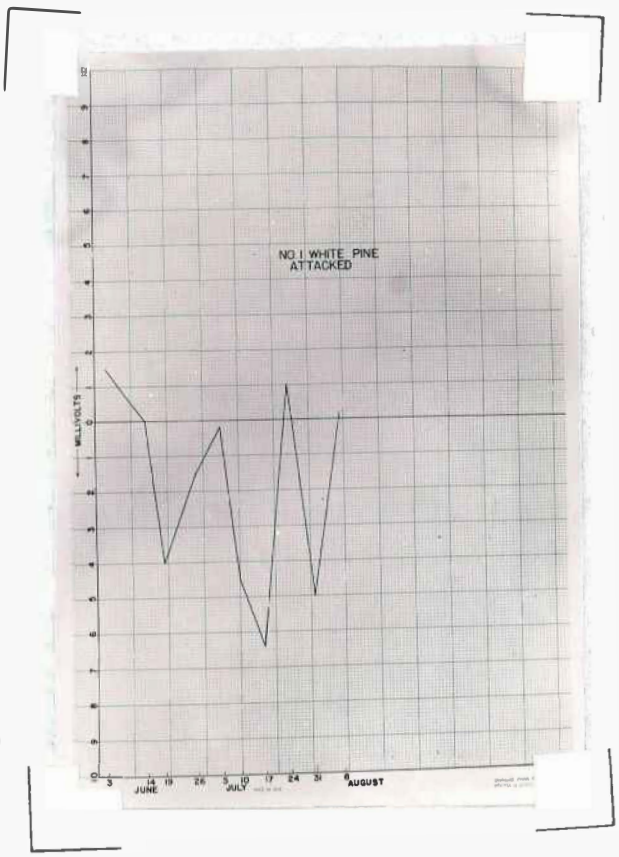

Figure 3. Tree number 1, white pine infested in 1939. In all cases the part of the ordinate above zero on the millivolt scale is positive; that is, the top of the tree was positive to the base. When the top became negative to the base, the line goes below zero.

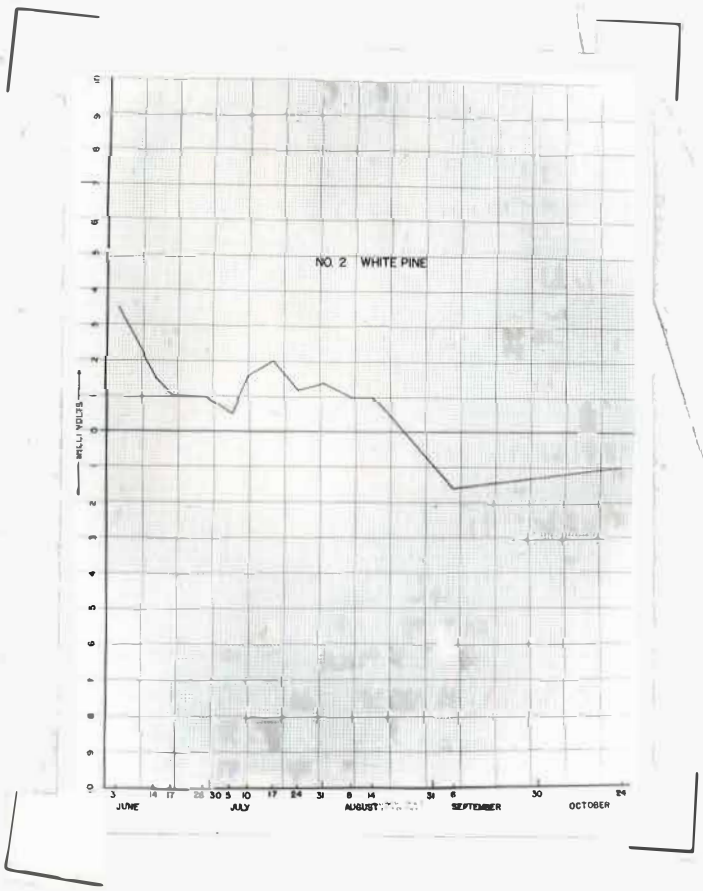

Figure 4. Tree number 2, white pine.
Uninfested and in good condition.

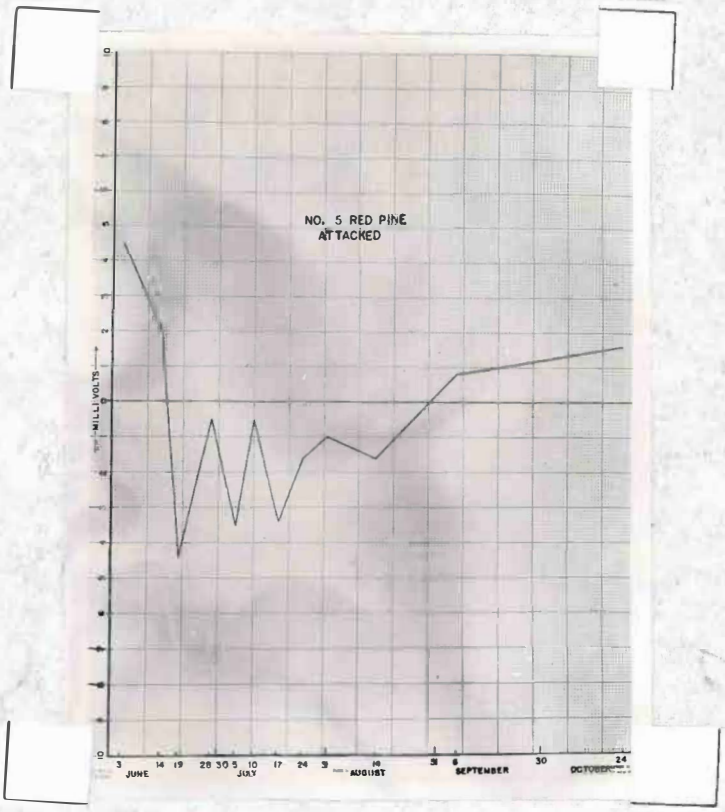

Figure 5. Tree number 5, red pine. Infested in 1939.

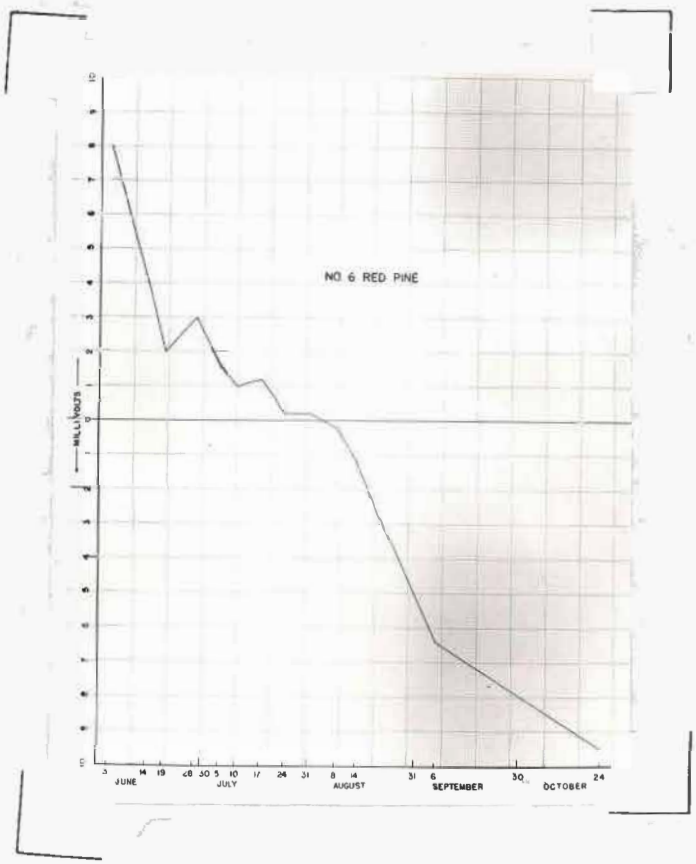

Figure 6. Tree number 6, red pine. Uninfested and in good condition.

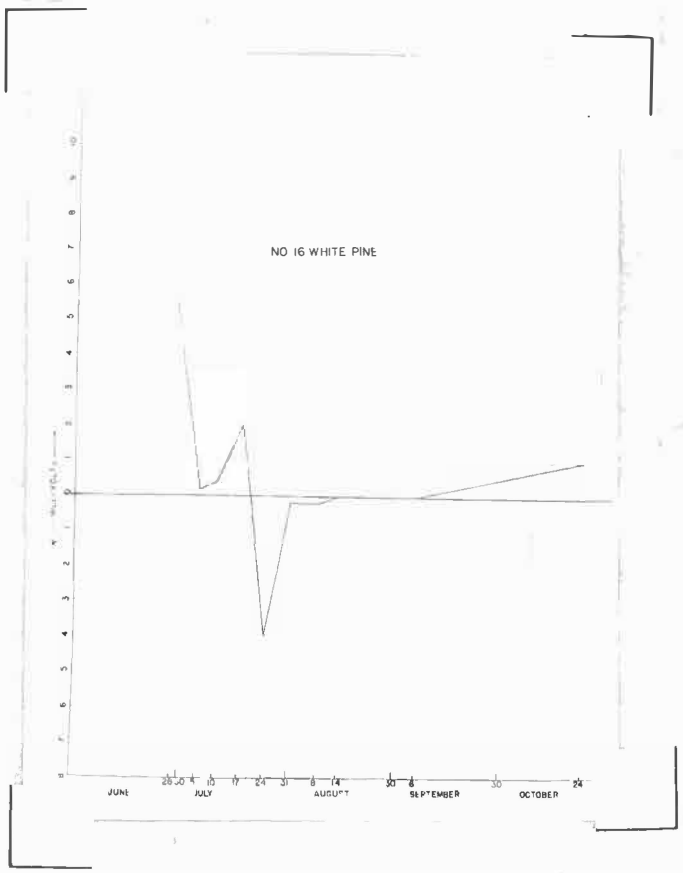

Figure 7. Tree number 16, white pine. Uninfested and apparently normal, but suppressed. The needles on this tree were yellow and the cambium brown nearly to the ground on October 24.